

1 Evidence for interacting but decoupled controls of  
2 decisions and movements in non-human primates  
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12 *Running head:*

13 Integrated control of decisions and movements in monkeys  
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35

## 36 Abstract

37 Many recent studies indicate that control of decisions and actions is integrated during  
38 interactive behavior. Among these, several carried out in humans and monkeys conclude that  
39 there is a co-regulation of choices and movements. Another perspective, based on human data  
40 only, proposes a decoupled control of decision duration and movement speed, allowing for  
41 instance to trade decision duration for movement duration when time pressure increases.  
42 Crucially, it is not currently known whether this ability to flexibly dissociate decision duration  
43 from movement speed is specific to humans, whether it can vary depending on the context in  
44 which a task is performed, and whether it is stable over time. These are important questions to  
45 address, especially to rely on monkey electrophysiology to infer the neural mechanisms of  
46 decision-action coordination in humans. To do so, we trained two macaque monkeys in a  
47 perceptual decision-making task and analyzed data collected over multiple behavioral sessions.  
48 Our findings reveal a strong and complex relationship between decision duration and movement  
49 vigor. Decision duration and action duration can co-vary but also “compensate” each other.  
50 Such integrated but decoupled control of decisions and actions aligns with recent studies in  
51 humans, validating the monkey model in electrophysiology as a means of inferring neural  
52 mechanisms in humans. Crucially, we demonstrate for the first time that this control can evolve  
53 with experience, in an adapted manner. Together, the present findings contribute to deepening  
54 our understanding of the integrated control of decisions and actions during interactive behavior.

55

## 56 New & noteworthy

57 The mechanism by which the integrated control of decisions and actions occurs, coupled or  
58 interactive but decoupled, is debated. In the present study, we show in monkeys that decisions  
59 and actions influence each other in a decoupled way. For the first time, we also demonstrate  
60 that this control can evolve depending the subject’s experience, allowing to trade movement  
61 time for decision time and limit the temporal discounting of reward value.

## 62 Keywords

63 Decision-making ; Arm movement ; Coordination; Non-human primates ; Reward value

## 64 Introduction

65 Recent theories and studies argue for an integrated control of decisions and actions during  
66 interactive behavior, at least when decisions are rapidly expressed through movements (Cisek  
67 and Kalaska, 2010; Shadmehr, 2010; Gallivan et al., 2018; Shadmehr et al., 2019). According  
68 to this framework, decisions, or factors guiding choices such as reward, time and effort,  
69 influence action parameters (Haith et al., 2012; Thura et al., 2014; Reppert et al., 2015;  
70 Summerside et al., 2018; Thura, 2020; Korbisch et al., 2022), and conversely, actions influence  
71 decisions (Cos et al., 2011; Burk et al., 2014; Morel et al., 2017; Michalski et al., 2020), even  
72 if the choice is about a sensory stimulus or reward harvest during foraging (Marcos et al., 2015;  
73 Hagura et al., 2017; Yoon et al., 2018; Reynaud et al., 2020; Saleri Lunazzi et al., 2021;  
74 Sukumar et al., 2023).

75 These observations are not compatible with a strict serial organization of behavior, where  
76 cognition, including decision-making is separate from perception and action, and lie between  
77 the two (Hurley, 2001). Instead, they support a dynamic control system operating in a closed  
78 loop where movements shape current and future potential actions (i.e. affordances), assigning  
79 various importance to the stimuli given such opportunities, and thus directly influencing  
80 decisions (Cisek, 2007; Buzsáki et al., 2014; Yin, 2014; Pezzulo and Cisek, 2016; Yoo et al.,  
81 2021).

82 While the integrated control of decisions and actions is an increasingly established hypothesis,  
83 a lively ongoing debate concerns the mechanism by which this integrated control occurs.

84 On the one hand, proposals have suggested that decisions and actions are jointly regulated,  
85 possibly by a common source (Thura et al., 2014; Thura, 2020; Carsten et al., 2023; Kita et al.,  
86 2023). Such “co-regulation” hypothesis, demonstrated in both humans and monkeys, is  
87 compatible with the older observations that reward and effort invigorate and slow down both  
88 decisions and actions, respectively (Kawagoe et al., 1998; Wickler et al., 2000; Milstein and  
89 Dorris, 2007; Xu-Wilson et al., 2009; Reppert et al., 2018; Summerside et al., 2018). It has been  
90 proposed that a regulation signal computed in the basal ganglia allows to maximize the rate of  
91 correct responses by jointly adjusting decisions urgency and action vigor during tasks involving  
92 multiple successive choices between actions (Thura et al., 2014, 2022; Thura and Cisek, 2017;  
93 Carland et al., 2019).

94 A second line of research suggests however that decision duration and movement speed are  
95 controlled independently of each other, allowing for instance to trade decision time for

96 movement time (Reynaud et al., 2020; Saleri Lunazzi et al., 2021, 2023; Herz et al., 2022). In  
97 support of this possibility, we recently showed that human subjects can shorten their decisions  
98 when an accurate and time-consuming movement is requirement (Reynaud et al., 2020; Saleri  
99 Lunazzi et al., 2021, 2023). We proposed that such adjustment is a “compensatory” mechanism  
100 established to decrease the temporal discounting of a positive outcome in each trial, and/or to  
101 limit a drop of success rate on a more global time scale. This ability to exchange decision  
102 duration for movement duration, i.e. the flexibility to dissociate decision urgency from  
103 movement vigor, argues for interacting but decoupled decision and motor control systems.

104 Importantly, it is not currently known whether this ability to flexibly dissociate decision  
105 duration from movement speed is specific to humans, maybe made possible by a sophistication  
106 of decision and motor neural circuits trough evolution, or whether non-human primates like  
107 old-world monkeys, who diverged from the human lineage about 25 MA ago, already have this  
108 skill. Likewise, it is currently not known if the regulation mechanism of decisions and actions  
109 is exclusive and stable over time or whether it can vary depending on the context in which a  
110 task is performed, and whether or not it can evolve with practice.

111 These are crucial questions to address because a significant part of what we know about the  
112 neural substrates of decision-making and motor control comes from (non-human) animal and,  
113 more specifically, monkey neurophysiology (Gold and Shadlen, 2007; Shenoy et al., 2013). It  
114 is thus important to figure out whether or not the mechanism underlying the integrated control  
115 of decision and movement (i.e. joint or compensatory) is similar in both species, stable across  
116 contexts and over time, first at the behavioral level in order to then rely on monkey  
117 electrophysiology to infer the neural mechanisms in humans.

118 In the present study, we trained two macaque monkeys to perform a decision between actions  
119 task and analyzed decision and movement data collected over dozens of sessions. We focused  
120 our analyses on the relationship between decision duration and movement vigor (speed and/or  
121 duration), both at the single trial level and between blocks of trials in which motor constraints  
122 were varied. We also investigated these relationships as a function of animals’ experience in the  
123 task. The analyses strongly indicate that decisions and actions influence each other, but in a  
124 decoupled way: decision duration and action vigor could co-vary but also “compensate” each  
125 other. Crucially, this integrated control can evolve with practice in an adapted manner. Our data  
126 indeed suggest that monkeys can trade movement time for decision time, and vice versa, when  
127 the total duration of behavior increases, possibly allowing to limit a drop of reward value due  
128 to temporal discounting.

## 129 Methods

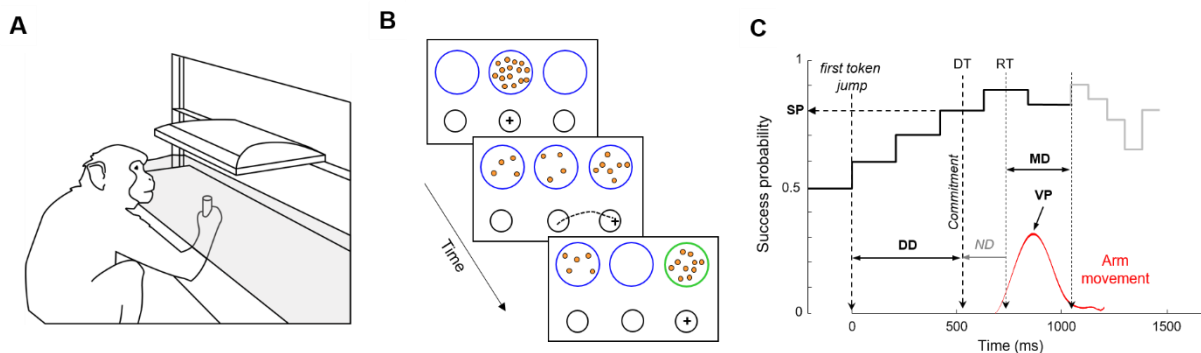
### 130 Subjects and ethics statement

131 The present report describes data collected from two rhesus macaque monkeys (*Macaca mulatta*  
132 - monkey G, female, 8 kg, 10 years old, right-handed; monkey B, male, 5 kg, 4 years old, left-  
133 handed). Ethical permission was provided by "Comité d'Éthique Lyonnais pour les  
134 Neurosciences Expérimentales" (CELYNE), C2EA #42, ref: C2EA42-11-11-0402-004.  
135 Monkey housing and care was in accordance with European Community Council Directive  
136 (2010) and the Weatherall report, "The use of non-human primates in research." Laboratory  
137 authorization was provided by the "Préfet de la Région Rhône-Alpes" and the "Directeur  
138 départemental de la protection des populations" under Approval Number: D69 029 06 01.

### 139 Experimental apparatus

140 The monkeys sat on a primate chair and made planar reaching movements using a lever held in  
141 their dominant hand (Fig. 1A). A digitizing tablet (GTCO CalComp) continuously recorded the  
142 lever horizontal and vertical positions (~100 Hz with 0.013-cm accuracy). Target stimuli and  
143 cursor feedback were projected by a VIEWPixx monitor (VPixx Technologies, 120 Hz refresh  
144 rate) onto a half-silvered mirror suspended 25 cm above and parallel to the digitizer plane,  
145 creating the illusion that targets floated on the plane of the tablet.

146



147 **Figure 1 - Experimental setup, task and data analysis.** A - Experimental apparatus. B - Time course of a trial in  
148 the task. C - Temporal profile of success probability in one example trial of the choice task. At the beginning of the  
149 trial, each target has the same success probability (0.5). When the first token jumps into one of the two potential  
150 targets (the most leftward vertical dotted line), success probability of that target increases to ~0.6. Success  
151 probability then evolves with every jump. Subjects execute a reaching movement (red trace) to report their choices.  
152 Movement onset (RT) and offset times are used to compute movement duration (MD). Peak velocity (VP) is  
153 determined as the maximum value between these two events. Movement offset marks the moment when the tokens  
154 that remain in the central decision circle jump more quickly to their assigned target (gray trace). The estimated time  
155 of the decision (DT) is computed by subtracting the subject's mean non-decision delay (ND) estimated in a simple  
156 delayed-reach (DR) task from movement onset time, allowing computation of the choice success probability (SP)  
157 at that moment. Only 10 out of 15 jumps are illustrated on this SP profile.  
158

159

160 Behavioral tasks

161 The monkeys performed the same task, a modified version of the “tokens task” (see Cisek et  
162 al., 2009 for the original version), as that performed by human subjects and for which data were  
163 reported recently (Reynaud et al., 2020) (Fig. 1B). They were faced with a visual display  
164 consisting of three blue circles (radius: 2.25 cm for monkey G; 2 cm for monkey B) placed  
165 horizontally at a distance of 6.375 cm (monkey G) or 7 cm (monkey B) from each other (the  
166 “decision” circles). In the central blue circle, 15 small tokens were randomly arranged.  
167 Positioned 5 cm (monkey G) or 5.5 cm (monkey B) below, three black circles, organized  
168 horizontally as well, defined the “movement” targets. The central black circle, the starting  
169 circle, remained constant at a radius of 1.5 cm, while the lateral black circles, positioned at a  
170 distance of 8 cm (monkey G) or 7 cm (monkey B) from the center, varied in size (radius: 1.25  
171 -1.75 cm; and 2.25 cm) in separate blocks of trials, resulting in two motor conditions (“small”  
172 vs. “large” targets).

173 A trial started when the animal moved and held the cursor in the black central circle for 500ms.  
174 At this point, the tokens began to jump one by one, every 200ms, from the central blue circle  
175 into one of the two possible lateral blue circles. The monkeys had to determine which of the  
176 two lateral blue circles would contain the majority of tokens before they had all jumped. They  
177 reported their decisions by moving the cursor into the corresponding lateral movement target  
178 (Fig. 1B). Importantly, monkeys could make and report their choices at any time between the  
179 first and last token jumps. However, the movement duration could not exceed 800ms, regardless  
180 of the motor condition. If the movement exceeded 800ms (too slow) or reached the target but  
181 failed to stop within 800ms (inaccurate), the trial was considered as a movement error and the  
182 movement target turned orange. When the choice was properly reported, the remaining tokens  
183 jumped more quickly to their final circles (Fig. 1C). This post-decision interval was set to 100-  
184 150ms and this acceleration of the remaining tokens implicitly encouraged animals to decide  
185 before all tokens had jumped into their respective lateral circles, aiming to save time and  
186 increase their reward rate. Note that this feature entails that movement duration carries a  
187 temporal cost with respect to the monkey’s rate of correct decisions because the remaining  
188 tokens accelerate at movement offset. The visual feedback regarding trial success (both correct  
189 decision and correct movement) or failure (correct movement but wrong decision) was provided  
190 after the last token jump, with the chosen decision circle turning green or red, respectively.  
191 Finally, the next trial began after a 1500ms inter-trial interval.

192 In addition to the tokens task, each animal had to complete trials in a delayed reach (DR) task  
193 in each session. The DR task was similar to the tokens task, but with only one lateral decision  
194 circle displayed at the beginning of each trial (on the right or left side of the central circle with  
195 a 50% probability). The tokens moved from the central circle to this unique lateral circle after  
196 a variable delay (400-550ms). Animals performed this task in the two different motor conditions  
197 (small and large targets). The DR task was employed to estimate the non-decision delay (ND,  
198 i.e. the sum of the delays attributable to sensory processing of the stimulus display) as well as  
199 to response initiation in each motor condition (Fig. 1C).

#### 200 Procedure

201 Sessions included in the present report were those during which monkeys were proficient in  
202 the task, typically following several months of training (see the stability of monkeys'  
203 performance in Fig. 2A). Data included in the analyses were collected over a total of 71 sessions  
204 for monkey G and 46 for monkey B. Each session consisted of alternating blocks (between 1  
205 and 5) of 10-60 correct trials in each motor condition whose order alternated on a daily basis.  
206 Monkeys had also to complete between 45 and 60 correct trials of the DR task in each condition.  
207 Monkeys performed as long as they remained motivated enough (mean  $\pm$  SD number of correct  
208 trials (both correct decisions and correct movements) for monkey G across sessions:  $174 \pm 62$ ;  
209 for monkey B:  $253 \pm 43$ ).

#### 210 Data analysis

211 All arm movement data were analyzed off-line using MATLAB (MathWorks). Reaching  
212 characteristics were assessed using the animals' movement kinematics. Horizontal and vertical  
213 position data were first filtered using a tenth-degree polynomial filter and then differentiated to  
214 obtain a velocity profile. Onset and offset of movements were determined using a 3.75 cm/s  
215 velocity threshold. Peak velocity (VP) was determined as the maximum value between these  
216 two events. To estimate the time at which monkeys committed to their choice (decision time,  
217 DT) on each trial, we detected the time of movement onset, defining the animal's reaction time  
218 (RT), and subtracted from it her/his mean non decision delays (ND) estimated based on her/his  
219 reaction times in the same motor condition (large or small targets) of the delayed reach task  
220 performed the same day. Decision duration (DD) was computed as the duration between DT  
221 and the first token jump (Fig. 1C). The task design allows to calculate, at each moment in time  
222 during a trial, the success probability  $p_i(t)$  associated with choosing each target  $i$  (Eq. 1). For  
223 instance, for a total of 15 tokens, if at a particular moment in time the right target contains  $N_R$   
224 tokens, whereas the left target contains  $N_L$  tokens, and there are  $N_C$  tokens remaining in the

225 center, then the probability that the target on the right will ultimately be the correct one, i.e., the  
226 success probability (SP) of guessing right is as follows:

$$p(R|N_R, N_L, N_C) = \frac{N_C!}{2^{N_C}} \sum_{k=0}^{\min(N_C, 7-N_L)} \frac{1}{k! (N_C - k)!} \quad (1)$$

227 To ensure that the difficulty of decisions was homogeneous among experimental conditions,  
228 especially between the two motor conditions, we controlled the sequence of trials experienced  
229 by animals in each session. We interspersed among fully random trials (30% of the trials in  
230 which each token is 50% likely to jump into the right or the left lateral circle) three special  
231 types of trials characterized by particular patterns of token jumps. Between 30 and 40% of trials  
232 were so-called “easy” trials, in which tokens tended to move consistently toward one of the  
233 circles. Around 20% of trials were “ambiguous,” in which the initial token movements were  
234 balanced, making the success probability of each target close to 0.5 until later in the trial. The  
235 last special trial type was called “misleading” trials (7-20%) in which the two to three first  
236 tokens jumped into the incorrect circle and the remaining ones into the correct circle (please  
237 refer to Thura and Cisek, 2014 - Figure 1, for a complete description of trial types criteria). In  
238 all cases, even when the temporal profile of token jumps of a trial was predesigned, the actual  
239 correct target was randomly selected on each trial. The rate of correct trials was computed for  
240 each session as the number of correct trials to complete in that given session divided by the sum  
241 of the durations of all trials performed to reach this requested number of correct trials.

## 242 Statistics

243 Wilcoxon rank sum tests are used to assess the difference in decision duration between  
244 categories of trials (e.g. easy versus ambiguous decisions). Pearson correlations are computed  
245 to assess the relationship between decision duration and movement parameters (speed and  
246 duration) at the single trial level, the session-by-session relationship between decision duration  
247 and action speed, and the relationship between the degree of coordination between decision  
248 duration and movement speed and the duration of decisions between sessions. For all statistical  
249 tests, the significance level is set a 0.05.

## 250 Results

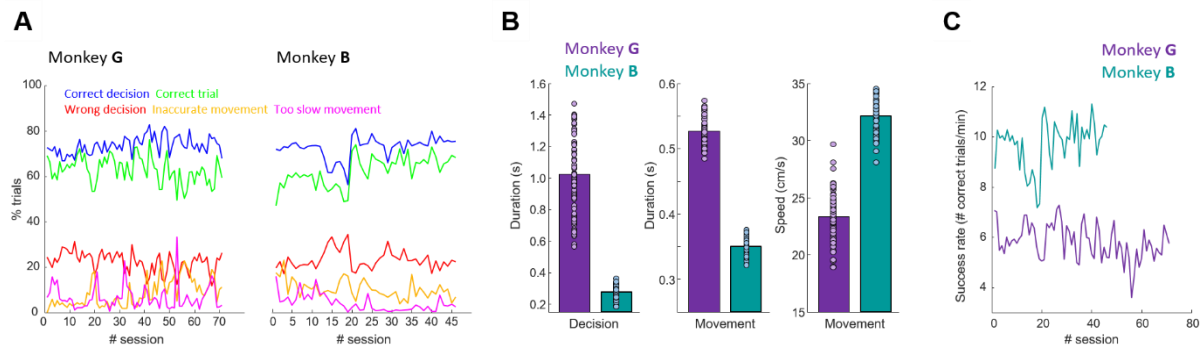
### 251 General observations

252 Over the 71 sessions performed by monkey G,  $63 \pm 6\%$  of the trials (mean  $\pm$  standard deviation  
253 between the sessions) were successful (both correct choices and correct movements). Without



254 taking into account the success of the movements,  $74 \pm 4\%$  of her decisions were correct.  
 255 Movement errors, too slow or inaccurate, were relatively sparse, representing  $7 \pm 5\%$  and  $8 \pm$   
 256  $6\%$  of the total trials, respectively. Monkey B's performance over the 46 sessions he completed  
 257 was comparable to that of monkey G.  $62 \pm 7\%$  of his trials were successful (correct decisions  
 258 and correct movements). Regardless of movement outcome,  $73 \pm 5\%$  of his choices were  
 259 correct.  $4 \pm 4\%$  of his movements were too slow,  $10 \pm 4\%$  were inaccurate. For both monkeys,  
 260 performance was stable across the sessions included in the present report (Fig. 2A).

261



262

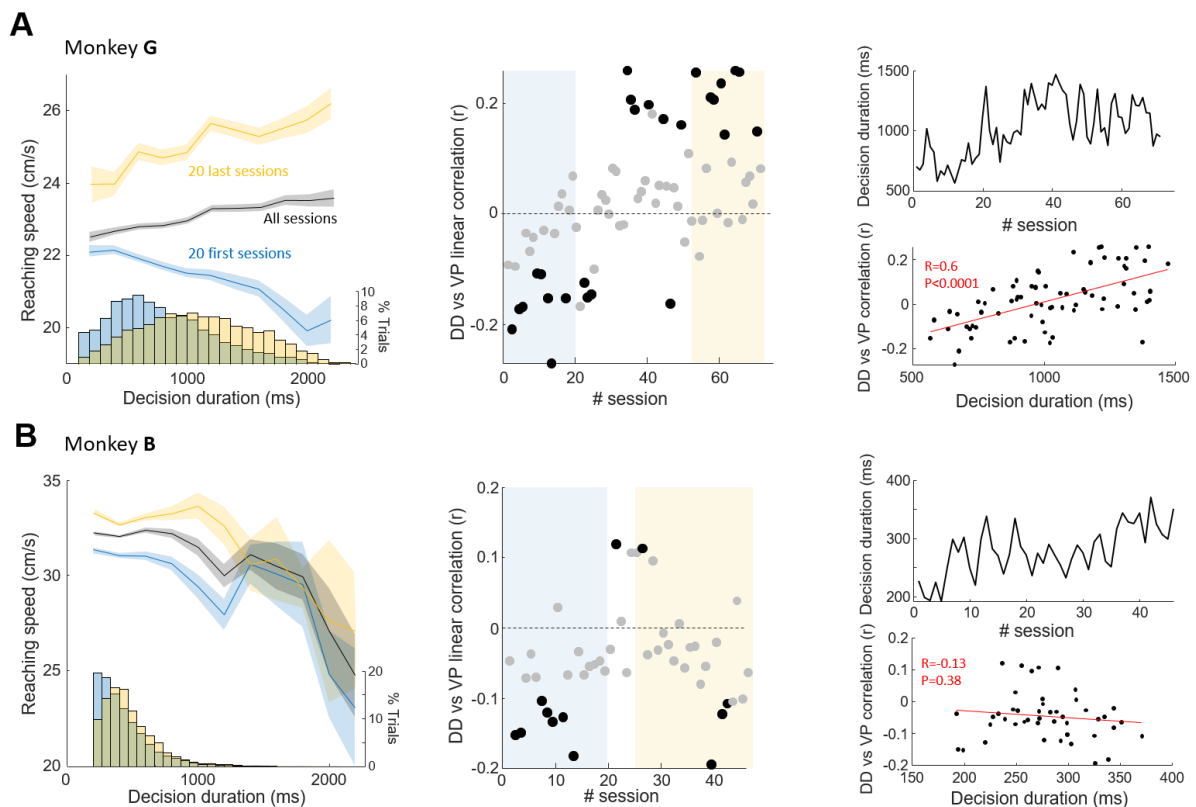
263 **Figure 2 - Global performance, decisional and movement vigor in the task.** A - Performance of each monkey  
 264 across sessions. B - Decision duration, reaching movement duration and speed for each of the two monkeys. Bars  
 265 illustrate mean values across sessions, and dots illustrate individual values for each session. C – Success rate of  
 266 each monkey across sessions.

267

268 Although their performance in the task is comparable, the analysis of animals' duration of  
 269 decisions, duration and speed of arm movements suggests that they used different strategies to  
 270 achieve these similar outcomes (Fig. 2B). On average, the duration of monkey G's decision  
 271 was  $1026 \pm 242\text{ms}$ . As expected, she decided more quickly when trials were easy compared to  
 272 when they were ambiguous ( $872 \pm 232\text{ms}$  vs.  $1154 \pm 259\text{ms}$ , Wilcoxon rank sum test,  $z = -5.7$ ,  
 273  $p < 0.0001$ ). To report her decisions, monkey G made arm movements whose duration was  
 274  $527 \pm 21\text{ms}$  and their speed was  $23 \pm 2 \text{ cm/s}$ . Monkey B was on average much faster to decide and  
 275 act compared to monkey G. His decision duration was  $249 \pm 43\text{ms}$ , with faster choices when  
 276 trials were easy compared to when they were ambiguous ( $230 \pm 40\text{ms}$  vs.  $369 \pm 73\text{ms}$ , Wilcoxon  
 277 rank sum test,  $z = -6.6$ ,  $p < 0.0001$ ). To report his decisions, monkey B made movements whose  
 278 speed was  $32 \pm 3 \text{ cm/s}$ , resulting in short duration actions ( $351 \pm 14\text{ms}$ ). As a consequence, the  
 279 rate of correct trials, defined for each session as the number of correct trials per minute (Fig.  
 280 2C), was much higher in monkey B than in monkey G ( $9.7 \pm 1$  correct trials/min vs.  $5.8 \pm 0.7$   
 281 correct trials/min).

282 Relationship between decision duration and movement vigor at the single trial level  
 283 To study the relationship between decision duration and arm movement vigor (speed and  
 284 duration) *within trials*, we first grouped all trials (correct and error trials, regardless of motor  
 285 condition) across sessions, separately for each monkey, according to decision time computed  
 286 in bins of 200ms, and calculated the mean ( $\pm$  standard error) values of movement parameters  
 287 in each bin.

288 The analysis of monkey G movement speed as a function of decision duration (including  
 289 decision durations until 2200ms, which corresponds to 99.6% of the trials) shows a slight but  
 290 continuous *increase* of movement speed with decision duration (from 22.5 to 23.9 cm/s, Fig.  
 291 3A, left panel). A linear regression through the data indicates a very strong and significant  
 292 relationship between the two variables (Pearson correlation,  $r=0.98$ ,  $p<0.0001$ ), with a positive  
 293 slope (0.14) and an intercept at 22.4 cm/s. No significant relationship between decision duration  
 294 and movement duration is observed (Pearson correlation,  $r=0.02$ ,  $p=0.9$ ).



295  
 296 **Figure 3 - Relation between decision duration and arm movement speed within trials.** A – Left panel: Speed  
 297 of monkey G’s arm movements (reaching) as a function of decision duration, computed in bins of 200ms, averaged  
 298 ( $\pm$  standard error, shaded areas) across all trials (black), trials of the 20 first sessions (“early” sessions, blue) and  
 299 trials of the 20 last sessions (“late” sessions, orange). Histograms at the bottom of the panel show the distributions  
 300 of the duration of monkey G’s decisions in the two groups, “early” and “late” sessions. Center panel: Pearson linear  
 301 correlation between the duration of monkey G’s decisions (DD) and arm movement speed (velocity peak, VP) as a  
 302 function of the session performed by the monkey. Each dot illustrates the value for a given session. The blue and  
 303 orange shaded areas highlight the 20 first and the 20 last sessions performed by monkey G, respectively. A negative  
 304 (positive)  $r$  value means that the longest the decision, the slowest (fastest) the movement. The black filled dots

305 mark sessions in which the correlation is significant. *Right panel, top*: Mean duration of monkey G's decisions within  
306 sessions, as a function of the session performed by the monkey. *Right panel, bottom*: Relationship between the  
307 Pearson correlation between decision durations and the speed of monkey G's movements and the mean duration  
308 of her decisions in each session. Each dot illustrates the value for a given session. The red line illustrates the result  
309 of a linear regression through the data. *B* – Same as in A for trials performed by monkey B.

310

311 By contrast, the analysis of the relationship between the duration of decisions and the speed of  
312 monkey B's movement within trials (including decision durations until 2200ms, which  
313 corresponds to 99.9% of the trials) shows a continuous *decrease* of movement speed with  
314 decision duration (from 32.2 to 25 cm/s, Fig. 3B, left panel). A linear regression through the  
315 data indicates a significant relationship between the two variables (Pearson correlation,  $r=-0.85$ ,  
316  $p=0.0008$ ), with a negative slope (-0.62) and an intercept at 34 cm/s. As for monkey G, no  
317 significant relationship between monkey B decision duration and movement duration is  
318 observed (Pearson correlation,  $r=-0.05$ ,  $p=0.9$ ).

319 We then asked whether this relationship between decision duration and movement speed within  
320 trials was stable over extended periods of time, depending on the monkeys' experience in the  
321 task, or if it could possibly evolve depending on this experience. To do this, we first carried out  
322 the same analyzes as those described above but with trials grouped according to the number of  
323 sessions performed by each monkey. For both animals, we compared trials collected during  
324 their first 20 sessions ("early" sessions) with those performed in their last 20 sessions ("late"  
325 sessions).

326 The relationship between the duration of decisions and the speed of monkey G's movements is  
327 strong and significant in both groups of trials ("early" sessions:  $r=-0.9$ ,  $p=0.001$ ; "late" sessions:  
328  $r=0.82$ ,  $p=0.0021$ ), but the slope is *negative* for "early" sessions (-0.22) and *positive* for "late"  
329 sessions (0.19). This means that the longest decisions were followed by the slowest movements  
330 during monkey G's first sessions and then, with practice, this relationship reversed. To better  
331 capture this evolution, we analyzed the session-by-session relationship between decision  
332 duration and action speed in monkey G and we found that a linear regression shows a strong  
333 and significant fit (Pearson correlation,  $r=0.61$ ,  $p<0.0001$ ), with a positive slope, meaning that  
334 the link between decision duration and movement speed continuously evolved through monkey  
335 G's practice (Fig. 3A, middle panel). In particular, among the first 20 sessions, decision  
336 durations were significantly correlated with movement speed in 8 sessions, always with long  
337 decisions followed by slow movements. Among the last 20 sessions, we found a significant  
338 correlation between decision duration and movement speed in 8 sessions too, but this time  
339 always with long decisions followed by rapid movements. Finally, we analyzed the duration of

340 monkey G's decision in the two groups of trials and noticed that with practice, she became  
341 more conservative and decided more slowly (mean  $\pm$  standard error; "early" sessions:  $760 \pm$   
342  $6\text{ms}$  vs. "late" sessions:  $1101 \pm 7\text{ms}$ , Wilcoxon rank sum test,  $z = -35$ ,  $p < 0.0001$ ) (Fig. 3A, left  
343 panel). Interestingly, we found a positive and significant correlation between the degree of  
344 coordination between decision duration and movement speed and the duration of decisions  
345 between sessions (Pearson correlation,  $r = 0.6$ ,  $p < 0.001$ ) (Fig. 3A, right panels). In other words,  
346 the emergence of the positive correlation between decision duration and movement speed (the  
347 longest the decision, the fastest the movement) within trials through practice coincides with the  
348 increase of the duration of monkey G's decisions through practice. In the supplementary section  
349 of the present report, we describe the relationship between the evolution of the correlation of  
350 decision duration and movement speed and the evolution of decision duration in two other  
351 monkeys who performed a similar version of the task (Fig. S1), strongly supporting the same  
352 conclusion (Fig. S2).

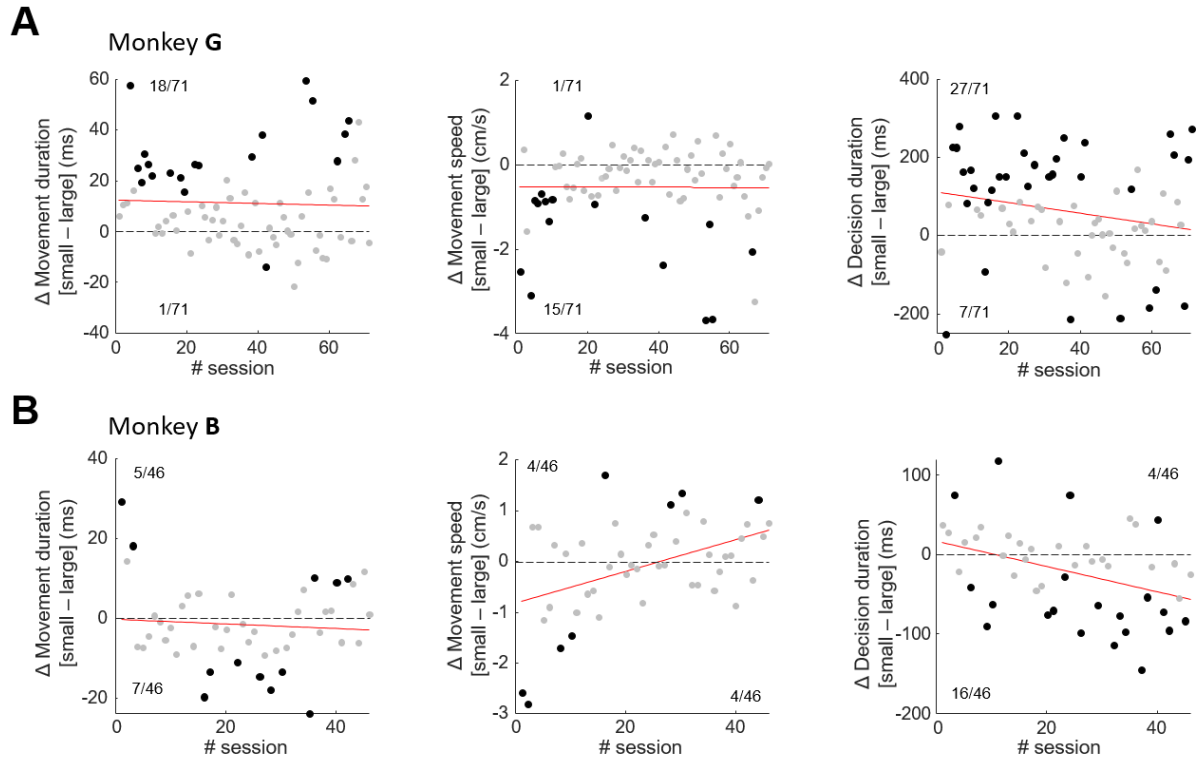
353 As for monkey G, the relationship between the duration of decisions and the speed of monkey  
354 B's movements is significant in both groups of trials ("early" sessions:  $r = -0.78$ ,  $p = 0.0044$ ; "late"  
355 sessions:  $r = -0.9$ ,  $p = 0.0002$ ). But contrary to monkey G, the slope is negative in both groups: -  
356  $0.65$  for "early" and  $-0.64$  for "late" sessions (Fig. 3B, left panel). This means that regardless  
357 of the monkey's level of experience in the task, the longest decisions were followed by the  
358 slowest movements. We did not find a particular link between the relationship between decision  
359 duration and action speed and the sessions performed by monkey B through his practice (Fig.  
360 3B, middle panel). Among the first 20 sessions, decision durations were significantly correlated  
361 with movement speed in 7 sessions, and always with long decisions followed by slow  
362 movements. Among the last 20 sessions, the correlation between decision duration and  
363 movement speed was significant in 3 sessions, still with long decisions followed by rapid  
364 movements. Interestingly though, despite the fact that the relationship between decision  
365 duration and movement speed *within trials* did not change with practice, we found that  
366 movement speed was overall higher in the "late" sessions group (intercept =  $35\text{ cm/s}$ ) compared  
367 to the "early" sessions one (intercept =  $32.9\text{ cm/s}$ ) (Fig. 3B, left panel). The analysis of the  
368 duration of monkey B's decision in the two groups showed that he was slightly more  
369 conservative in the "late" sessions compared to the "early" sessions ( $302 \pm 3\text{ms}$  vs.  $259 \pm 3\text{ms}$ ,  
370 Wilcoxon rank sum test,  $z = -17$ ,  $p < 0.0001$ ) (Fig. 3B, left panel). Contrary to monkey G, no  
371 significant relationship between the degree of coordination between decision duration and

372 movement speed and the duration of monkey B's decisions between sessions is observed (Fig.  
373 3B, right panels).

#### 374 Effect of motor constraints on the relationship between decision and action

375 Another way to study the coordination between decision duration and movement vigor is to  
376 encourage animals to vary the vigor of their movements in blocks of trials and assess the  
377 consequence of this adjustment on decision duration. A co-regulatory mechanism predicts that  
378 slowing movements will be accompanied by slowing decisions, while a more flexible  
379 mechanism could be demonstrated by observing shortened decisions when movements are  
380 longer, as we have seen in humans (Reynaud et al., 2020; Saleri Lunazzi et al., 2021, 2023).

381 Across all sessions, when movements were correctly executed (decisions could be correct or  
382 wrong), the speed of monkey G's movements was slower (mean speed  $\pm$  standard error:  $22.8 \pm$   
383  $0.05$  cm/s vs.  $23.3 \pm 0.05$  cm/s, Wilcoxon rank sum test,  $z = -6$ ,  $p < 0.0001$ ) and their duration  
384 longer ( $536 \pm 1$  ms vs.  $525 \pm 1$  ms,  $z = 8.4$ ,  $p < 0.0001$ ) when they were executed toward the small  
385 targets ("small" target block) compared to when they aimed to the large targets ("large" target  
386 block). We found that the duration of monkey G's decisions was overall slower when  
387 movements were directed toward small targets compared to when they reached the large targets  
388 ( $1020 \pm 6$  ms vs.  $953 \pm 6$  ms,  $z = 8.6$ ,  $p < 0.0001$ ). At the session level, we found a significant  
389 effect of the motor condition on the speed and duration of monkey G's movements in 16 and  
390 19 out of 71 sessions, respectively (Wilcoxon rank sum test,  $p < 0.05$ ), with movements being  
391 faster and shorter when directed to the large targets in 15/16 and 18/19 cases, respectively (Fig.  
392 4A, left and middle panels). The duration of monkey G's decisions was modulated by the motor  
393 condition in 34 out of 71 sessions (Wilcoxon rank sum test,  $p < 0.05$ ), with decisions being  
394 slower when movements were slower in the majority of cases (27/34) (Fig. 4A, right panel).  
395 Interestingly, we found that this tendency to slow down decisions when a time consuming  
396 movement was necessary diminished with practice. Indeed, while the effect of the motor  
397 condition on movement speed and duration was stable over monkey G's practice (Fig. 4A, left  
398 and middle panels), the number of sessions during which long decisions preceded long  
399 movements decreased (20 over the first 35 sessions; 5 for the last 35 sessions) (Fig. 4A, right  
400 panel).



401

402 **Figure 4 - Effect of motor constraints on arm movement vigor and decision duration.** *A – Left panel:*  
 403 *Difference of arm movement duration between trials of the small target blocks and those of the large target blocks,*  
 404 *as a function of the session performed by monkey G. Each dot illustrates data of a given session, and the black*  
 405 *dots mark sessions in which the difference is statistically significant (the number of statistically significant cases is*  
 406 *reported for each difference direction). A positive value indicates that movements were longer when they were*  
 407 *executed toward the small targets compared to when they were executed toward the large targets. The red line*  
 408 *illustrates the result of a linear regression through the data. Center panel: Same as in A for the difference of the*  
 409 *speed of monkey G’s arm movement between the two motor conditions. Right panel: Same as A for the difference*  
 410 *of the duration of monkey G’s decisions between the two motor conditions. B – Same as in A for trials performed*  
 411 *by monkey B.*

412

413 The effect of target size on the speed and duration of monkey B’s movement is less clear, at  
 414 least when trials are grouped across sessions. Movement speed was not significantly modulated  
 415 as a function of the motor condition (small vs. large target:  $32 \pm 0.07$  cm/s vs.  $32.2 \pm 0.07$  cm/s,  
 416 Wilcoxon rank sum test,  $z = -0.2$ ,  $p=0.8$ ). Movement duration was slightly longer when  
 417 movement reached the large targets compared to when they reached a small target ( $349 \pm 0.7$ ms  
 418 vs.  $351 \pm 0.7$ ms;  $z = -2.3$ ,  $p=0.02$ ). At the session level, the effect of target size on the kinematics  
 419 of monkey B’s movements (duration and speed) was mixed, as can be seen in figure 4B, left  
 420 and middle panels. However, target size significantly modulated decision duration in 20 out of  
 421 46 sessions (Wilcoxon rank sum test,  $p<0.05$ ). In the majority of cases (16/20), decision  
 422 duration was longer when movements reached the large targets (Fig. 4B, right panel).  
 423 Interestingly, with practice, this monkey progressively decreased his movement speed in one  
 424 condition (“large” target block) compared to the other one (“small” target block) (Fig. 4B,

425 middle panel), and this relative decrease of speed was accompanied by a session-by-session  
426 lengthening of decisions in the large target blocks compared to the small target blocks (Fig. 4B,  
427 right panel). The link between these two adjustments from one session to the next is significant  
428 (Pearson correlation,  $r=-0.3$ ,  $p=0.03$ ).

## 429 Discussion

430 In the present report, we show in non-human primates that the duration of perceptual decisions  
431 and the speed of the arm movements executed to report these choices are often correlated at the  
432 single-trial level. The results support an interacting but decoupled control of the decision-  
433 making and movement execution processes: decision duration and action speed are sometimes  
434 co-regulated (the slower the decision, the slower the movement), and they sometimes  
435 “compensate” each other (the slower the decision, the faster the movement). We also  
436 demonstrate that the degree and direction of coordination between decision duration and  
437 movement vigor can evolve, particularly as a function of the overall duration of the animals'  
438 decisions in each session: the “compensatory” mode of regulation comes into play as duration  
439 of choices increases. Finally, we show that when the motor context encourages time-consuming  
440 movements, decision duration and movement vigor are often co-regulated. This context-  
441 dependent relationship also appears flexible depending on the animals’ experience in the task.

442 These observations agree with many recent experimental results that challenge the classic view  
443 of behavior organization (Pylyshyn, 1984), in which perception, decision, and action are  
444 considered as independent, temporally separate and serial processes (Hurley, 2001). More and  
445 more studies indeed show that decisions and actions are closely interconnected and influence  
446 each other, at least during rapid interactive behavior (Cos et al., 2011; Haith et al., 2012; Burk  
447 et al., 2014; Marcos et al., 2015; Reppert et al., 2015; Hagura et al., 2017; Morel et al., 2017;  
448 Summerside et al., 2018; Yoon et al., 2018; Michalski et al., 2020; Reynaud et al., 2020; Thura,  
449 2020; Saleri Lunazzi et al., 2021, 2023; Korbisch et al., 2022; Carsten et al., 2023; Kita et al.,  
450 2023; Sukumar et al., 2023).

451 A particularly interesting question concerns the mechanism by which such integrated control  
452 of decisions and actions occurs. On the one hand, decisions and actions might be coupled,  
453 jointly regulated by a common source (Thura et al., 2014; Thura, 2020; Carsten et al., 2023;  
454 Kita et al., 2023). According to this hypothesis, in a context encouraging decision speed, the  
455 fastest choices will be reported with the fastest movements. Similarly, if a decision needs to be  
456 reported with a slow and careful movement, this decision will tend to be longer than that

457 expressed by a rapid movement. A second line of research suggests however that the control of  
458 decision duration and movement speed is decoupled, allowing to trade decision time for  
459 movement time if necessary (Reynaud et al., 2020; Saleri Lunazzi et al., 2021, 2023; Herz et  
460 al., 2022). At the origin of this second hypothesis, we showed that human subjects can shorten  
461 their decisions when an accurate and time-consuming movement is required (Reynaud et al.,  
462 2020; Saleri Lunazzi et al., 2021, 2023). We proposed that such adjustment is a compensatory  
463 mode possibly established to prevent the temporal discounting of a positive outcome in each  
464 trial, and/or to limit a drop of success rate on a more extended time scale. Interestingly, in two  
465 recent studies specifically designed to address the mode of regulation of decisions and actions  
466 (Carsten et al., 2023; Kita et al., 2023), and whose results support a co-regulation mechanism,  
467 decision and movement durations had no impact on the participants' success rate (i.e. it was not  
468 adaptive in terms of success rate to speed up movements after a long decision for instance),  
469 unlike the design of the experiments described in Reynaud et al. (2020) and Saleri Lunazzi et  
470 al. (2021, 2023).

471 The data presented in this report suggest for the first time that both modes of coordination can  
472 be used by the same subject. At the single trial level, the slowest decisions made by monkey B  
473 were expressed with the slowest movements (Fig. 3B, left panel), a result consistent with a co-  
474 regulation of decisions and actions. Monkey G also co-regulated but mostly during the first  
475 sessions she performed. With experience, the relationship between the duration of her decisions  
476 and the speed of her movements reversed, consistent with a decoupled, "compensatory" mode  
477 of regulation of choices and actions (Fig. 3A, left panel). With trials grouped as a function of  
478 animals' experience, we found in both monkeys that decisions were slower in the late sessions  
479 compared to the early sessions, and these slower decisions were reported with faster movements  
480 (Fig. 3A-B, left panels), a pattern of results also consistent with a "compensatory" mode of  
481 regulation of decisions and actions. Finally, with trials grouped according to the motor context  
482 in which decisions were made (i.e. small vs. large targets), we found evidence for a co-  
483 regulation of decisions and actions, with slow movements often preceded by slow decisions,  
484 with a trend for an evolution toward a "compensatory" mode in monkey G (Fig. 4A). The way  
485 in which the duration of the decision and the vigor of the action are coordinated thus appears  
486 complex, flexible and dynamic depending on the context in which the task is carried out. In the  
487 following paragraph, we discuss the possible reasons which could explain the use of these  
488 different modes of coordination.



489 It is well-established that individuals tend to exhibit a preference for policies that maximize  
490 their rate of correct responses when faced with multiple successive decisions (Bogacz et al.,  
491 2010; Balci et al., 2011). Several factors influence this success rate, with time being a crucial  
492 one, as evidenced by the well-known concept of temporal discounting of reward value  
493 (Myerson and Green, 1995). Because both decisions and actions are time consuming processes,  
494 minimizing the time required to obtain a reward likely leads to adaptations concerning both  
495 decisions and movements. A decoupled yet interconnected control of decisions and actions  
496 provides individuals with the ability to adapt both deliberation and movement speed together,  
497 minimizing the time it takes to achieve a given goal. Moreover, this mode also possesses the  
498 flexibility to selectively adjust one aspect while preserving the integrity of the other. For  
499 instance, during easy decisions, deliberation time can be slightly sacrificed when accurate and  
500 slow response movements are required (Reynaud et al., 2020; Saleri Lunazzi et al., 2021, 2023).  
501 The present results indicate that just like humans, monkeys also have the ability to flexibly  
502 adjust the way they coordinate their decisions with their actions, in particular according to their  
503 experience in the task.

504 The evolution of the coordination between decision duration and action vigor depending on  
505 animals' experience is particularly useful in revealing the principles underlying how these two  
506 processes are controlled. Crucially, the emergence of the compensatory mode of coordination  
507 always coincides with an increase of the duration of the animal's overall behavior (Fig. 3A,  
508 right panel; Fig. S2). This is particularly salient in monkey G who showed an important increase  
509 in her decision durations over the course of the sessions carried out (Fig. 3A, right panel).  
510 Interestingly, the subtle and gradual decoupling of decision and action observed across sessions  
511 between large and small target conditions (Fig. 4A, right panel) occurs simultaneously with the  
512 overall lengthening of her decision durations across sessions (Fig. 3A, top right panel). She  
513 may have wanted to seek to compensate for her long movements by limiting the increase in the  
514 duration of her decisions in the most constrained motor blocks (i.e. small target). By contrast,  
515 monkey B, who was constantly very fast to decide and act, showed almost no sign of  
516 compensation between decision and movement durations. In monkey S and monkey Z who  
517 were even slower to decide than monkey G, the coordination within trials between decision  
518 duration and action speed is only of the compensatory type, but it still depends on the duration  
519 of the animals' overall decisions (Fig. S2). We thus propose that the decoupled, compensatory  
520 mode of regulation is highly adaptive in the sense that it allows to deal with deadlines and/or  
521 makes it possible to limit the temporal discounting of the reward value in each trial. In the

522 longer term, it could also help optimize the overall success rate of the animals in each session.  
523 Between these three possibilities, we lean toward the limitation of the temporal discounting of  
524 the reward value in each trial because (1) monkeys almost never failed their trials because of  
525 responding after 3s (i.e. the deadline of deliberation) and (2) the overall success rate of monkey  
526 G does not appear to improve despite the emergence of the compensatory mode of regulation  
527 across sessions (Fig. 2C).

528 The different strategies adopted by the two monkeys can be explained by their very different  
529 personalities and backgrounds. Monkey B who faced his first experimental task is much  
530 younger than monkey G. He adopted such a fast and impulsive behavior that there was almost  
531 no temporal discounting of reward in each (correct) trial, and no room for either decision or  
532 movement duration shortening. Consequently, a decoupled mode of regulation that would  
533 compensate for slightly longer decisions or movements to meet some reward rate maximization  
534 principles was probably irrelevant to this monkey. Monkey G however, who is older and more  
535 experienced in laboratory experiments, exhibited a more conservative and less vigorous  
536 behavior. Therefore, she had to face higher temporal discounting of reward in each trial and  
537 lower reward rate at a more global scale (Fig. 2C). Compensation between decision and  
538 movement duration becomes beneficial in this case.

539 Human subjects having performed the same task show a compensatory mode of coordination  
540 of decision and action when the trials are grouped according to the motor constraints imposed  
541 on the subjects (Reynaud et al., 2020). By contrast, with the same comparison (decision  
542 durations between small versus large target conditions), we report here that monkeys tend to  
543 primarily exhibit a co-regulation of decisions and actions. This difference between monkeys  
544 and human subjects can be explained by at least two factors. Firstly, monkeys received drops  
545 of juice at each correct trial as a reward, so their strategy was probably primarily driven by the  
546 prospect of receiving this strong primary reinforcer. By contrast, humans did not receive instant  
547 rewards. Their motivation was likely more oriented toward the completion of the required  
548 number of correct trials as quickly as possible, aiming to maximize their overall success rate at  
549 the sessions level. Another, not mutually exclusive explanation is that taking the motor context  
550 into account to compensate for movement duration during the decision-making process requires  
551 a significant level of abstraction that monkeys can only gradually acquire with training and  
552 experience, to eventually exploit it in an adapted manner. Interestingly, we report that with  
553 practice, the slowdown of monkey G's decisions reported with slow movements in specific  
554 blocks of trials tends to decrease (Fig. 4A). By mastering the timing parameters of the task over

555 the sessions, she may have realized that beyond accuracy at the single trial level, she could also  
556 optimize her time spent in a session by slightly reducing the duration of her decisions when  
557 movements were slow, just as human subjects did, with the difference that they were able to do  
558 it after just one session.

559 In previous experiments in which humans and monkeys were tested in a task similar to that  
560 described in the present report, we proposed that both decision urgency and movement vigor  
561 (Thura et al., 2014; Thura, 2020) were co-regulated. This conclusion was based on two  
562 observations. At the single trial level first, early decisions (usually made on the basis of strong  
563 sensory evidence but low urgency) were followed by long duration movements whereas later  
564 decisions (relying on weak sensory evidence but stronger urgency) were followed by shorter  
565 and faster movements, as if they were influenced by the strong level of urgency encountered  
566 when a significant amount of time has elapsed during a trial. Second, when subjects were  
567 encouraged to make earlier and less accurate decisions in blocks of trials (fast speed-accuracy  
568 trade-off (SAT) regime), we observed faster movements compared to a condition where  
569 accuracy was emphasized. The multiple modes of regulation of decisions and actions that we  
570 report in the present study suggest however that the mechanism underlying the control of  
571 decision duration and movement speed is more elaborated than being under the influence of a  
572 single regulation signal. Indeed, while a shared signal may control decision and movement  
573 durations at the single trial level (especially when fast movements follow long decisions), and  
574 between different decisional SAT regimes, a unique signal cannot account for the fact that the  
575 movements executed following the slower decisions made during the late sessions were faster  
576 compared to those made during the early sessions during which decision were faster. Together,  
577 these observations suggest the involvement of multiple sources of regulation of decisions and  
578 actions, likely implemented by diverse brain circuits, and used differently and specifically  
579 depending on the context in which a task takes place.

580 Electrophysiological data have highlighted an overlap of brain regions involved in decision-  
581 making and those of action processes, particularly in the sensorimotor cortex and the basal  
582 ganglia (Gold and Shadlen, 2007; Cisek and Kalaska, 2010; Robbe and Dudman, 2020). Studies  
583 suggest, for example, that activity in the internal section of the globus pallidus, the output  
584 nucleus of the basal ganglia, determines decision urgency (Thura and Cisek, 2017; Thura et al.,  
585 2022) as well as movement vigor (Turner and Desmurget, 2010; Dudman and Krakauer, 2016;  
586 Yttri and Dudman, 2016). In the present study, we describe a within trial level of coordination  
587 between decisions and actions possibly established to deal with deadlines and promote the value

588 of the immediate reward. This mechanism might be implemented within the cortico-basal  
589 ganglia-thalamo-cortex circuits, with the dopamine as a transmitter dedicated to the exploitation  
590 of the local reward opportunities (Niv et al., 2007). Interestingly, a recent study conducted by  
591 Herz and colleagues (2022) shows that the subthalamic nucleus (STN) can independently  
592 control movement and decision speed in distinct time windows, a result that is compatible with  
593 the contribution of this basal ganglia nucleus to the decoupled coordination of decisions and  
594 actions that we report at the behavioral level in the present study. We also propose that the  
595 different modes of coordination of decisions and actions may serve more global, abstract goals  
596 such as the optimization of the rate of successes at the session level. This mechanism might be  
597 implemented in broader circuits under the regulation of neuromodulation systems, such as the  
598 noradrenergic circuits (Murphy et al., 2016; Steinemann et al., 2018; Kaduk et al., 2023).  
599 Another possibility, not mutually exclusive, is that structures known to perform predictive  
600 computing and build internal models of the world, such as the cerebellum, would play a role in  
601 such long term goal establishment (Pezzulo and Cisek, 2016; Kruithof et al., 2023), by building  
602 internal models of behavior utility in each task, allowing to optimize the global value of  
603 behavior over extended time scales.

604

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